

Conodont
Ultrastructure:
The Family
Panderodontidae

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Publication date: 15 June 1973

Suggested citation: Life Sci. Contr., R. Ont. Mus.

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PRICE: \$2.00

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100 Queen's Park, Toronto, Canada

PRINTED AT THE UNIVERSITY OF TORONTO PRESS

Conodont Ultrastructure: The Family Panderodontidae

Abstract

The ultrastructure of representative specimens of 11 form species of the conodont genera *Panderodus* and *Belodina*, comprising the family Panderodontidae, was investigated using oriented, etched sections examined primarily with the scanning electron microscope. Selected species are of wide stratigraphic and geographic occurrence. Details of the form and pattern of crystallites and lamellae permitted interpretation of the mode of growth of both genera. Critically important is the discovery of radial as well as concentric lamellae. The former, flanking the longitudinal furrow on the inner lateral face and having surface expression as coarse striations, represent a radically different form of element construction not documented, although suspected in other, simple-cone genera. Lamellae constructing the basal rim commonly are restricted to the basal region. Development of white matter is considered to be functionally advantageous by limiting the amount of potential element damage to the cusp and denticle tips. Holes within the lamellar basal filling are considered to be primary. The similarity in ultrastructure between *Panderodus* and *Belodina* supports the recent establishment of the family Panderodontidae as a natural, taxonomic unit.

Introduction

Ultrastructure is now recognized as an important criterion to define and to distinguish suprageneric taxa of conodonts. Our earlier work (Barnes *et al.*, 1970; Barnes, Sass and Monroe, in press) documented the ultrastructure of a wide range of form taxa of Ordovician conodonts, using geographically widespread collections from a restricted geological time interval. We established certain basic properties of the crystallites, lamellae, white matter, and surface micromorphology. Differences in ultrastructure were documented between hyaline, neurodont (a subgroup of the hyaline conodonts), and cancellate (with extensive white matter) conodonts. The only significant feature attributable to geographic variation that we found may have been the extent to which white matter is developed in certain taxa, in contrast to others in which the proportion is constant.

Recently we examined the ultrastructure of certain distinctive conodonts that appear to be closely related and investigated possible variation in ultrastructure of examples through their geologic range. We examined Cambrian,

Ordovician, Silurian, and Triassic conodonts. This paper (see Barnes *et al.*, 1970, p. 3) deals with the ultrastructure of one of the most common widespread Ordovician genera, *Panderodus* Ethington (Fig. 3A-D) and a closely related genus, *Belodina* Ethington (Fig. 4F-H). Both originated in the early Middle Ordovician, *Belodina* ranging to the end of the Ordovician and *Panderodus* continuing into the Devonian. These genera are especially common in the North American Midcontinent Province, and details of their stratigraphy and ecology were discussed by Sweet *et al.* (1971), Seddon and Sweet (1971), and Barnes, Rexroad, and Miller (in press). Both form genera were established first by Ethington (1959) and considered in a multi-element concept by Bergström and Sweet (1966), Schopf (1966), and Webers (1966). *Panderodus* was emended by Clark and Ethington (1966) and recently revised by Ziegler and Lindström (1971).

In his suprageneric classification of conodonts, Lindström (1970, p. 433) included the following subdivision:

Superfamily	Panderodontacea Lindström
Family	Acanthodontidae Lindström
Subfamily	Acanthodontinae Lindström
Subfamily	Protopanderodontinae Lindström
Family	Panderodontidae Lindström

Subsequently Lindström and Ziegler (1971, p. 12) informally suggested that the two subfamilies of Acanthodontidae should be treated as separate families. Although the subdivision may require future revision, the family Panderodontidae appears to be a valid taxon containing the multi-element genera *Panderodus*, *Neopanderodus*, and *Belodina*. Lindström and Ziegler (1971) investigated the ultrastructure of members of the superfamily Panderodontacea and based their observations on 15 specimens that were fractured artificially to reveal aspects of the inner and outer structure. For the family Panderodontidae they used specimens of the form species *Panderodus gracilis* (Branson and Mehl), *P. simplex* (Branson and Mehl), *P. unicostatus* (Branson and Mehl), *Neopanderodus perlineatus* (Ziegler and Lindström), and *Belodina grandis* (Stauffer). Results of our concurrent work agree generally with their conclusions, but our techniques of preparation revealed more of the structure, permitted a more detailed interpretation of ultrastructure, and resulted in the discovery of a pattern of conodont growth not recognized before.

Species of *Panderodus* and *Belodina* are common in Middle and Upper Ordovician faunas from shelf carbonates overlying the Precambrian Shield in many areas of Canada and are presently under study by Barnes. They are especially abundant in northern and western Canada, where species are associated with the Arctic Ordovician fauna (e.g., Nelson, 1959).

Apparatuses of both multi-element genera consist of one, two, or three element types, depending on the species. Most panderodid, multi-element species (see Fig. 3A-D) have two element types: a round, slender form, e.g. *P. gracilis* (Branson and Mehl) *s.f.* and a broad, more compressed

element whose anterior margin is more regularly curved, e.g. *P. compressus* (Branson and Mehl) *s.f.* (Note that *s.f.*, i.e. *sensu formae*, is used herein to distinguish a form taxon from a multi-element taxon, as recommended by a majority of specialists attending the Marburg Symposium in Conodont Taxonomy in Germany, September 1971.) Homologues of these two element types are recognizable in most belodinid species. For example, *B. compressa* is composed of *B. grandis* (Stauffer) *s.f.* (Fig. 4G,H) and *B. compressa* (Branson and Mehl) *s.f.* (Fig. 4E,F) but also has a third component: a smaller, non-denticulate, strongly recurved element, *Eobelodina fornicata* (Stauffer) *s.f.* Apparatuses of *Panderodus* and *Belodina* are thus similar. Partial, fused apparatuses were described by Pollock (1969) for the former and by Barnes (1967a) for the latter.

Certain specimens of *Panderodus* spp., normally a non-denticulate, simple cone, developed germ denticles along the posterior margin (see, for example, Schwab, 1969). A more complete gradational series, ranging from panderodid to belodinid forms, has been observed in Barnes' collections. Although the form genera *Belodina* and *Eobelodina* were defined by Ethington (1959) and Sweet *et al.* (1959), respectively, to possess bifid basal cavities, this is not true for all species. Some have a single, deep cavity, as in panderodids. Morphology is thus similar in *Panderodus* and *Belodina*.

It has been known for many years (see Stauffer, 1935) that the outer surface of specimens of the two genera bear fine striations, which have been better illustrated with scanning electron microscope (SEM) photographs (Via, 1970; Lindström and Ziegler, 1971). Striations are most prominent on each side of a deep, narrow, lateral groove (Fig. 3H). Similar fine, longitudinal striations occur in specimens of several Ordovician simple-cone genera, especially *Scolopodus* (*sensu* Lindström, 1971, p. 40–41) and notably *S. gracilis* Ethington and Clark. Hence, *Panderodus* and *Belodina* share many common features and are clearly closely related. They differ principally in dentition and, to a lesser extent, in the occurrence of a bifid, basal cavity in species of *Belodina*. A similarity in ultrastructure would further support their close relationship and the validity of the family Panderodontidae.

Techniques and Material

Techniques of study are the same as those described previously (Barnes *et al.*, 1970; Barnes, Sass and Monroe, in press). Specimens were embedded in a bioplastic medium, ground to the desired level and orientation, polished with 0.003 μ aluminum oxide powder, etched for 20 seconds in 2N HCl, and then examined with the Cambridge Stereoscan Mark IIA (Cambridge Instrument Co., Cambridge, England).

Lindström and Ziegler (1971), who artificially fractured their specimens and examined the resulting surfaces, criticized etching techniques, and suggested that secondary fine structures could be simulated that did not conform to the original structure. A discussion of both methods is pertinent. Fracture surfaces should allow study of unaltered structure but present disadvantages and limitations. Conodont specimens do not readily fracture

along all desired directions. The arrangement of the crystallites and lamellae produces preferred lines of fracture. Hyaline conodonts fracture lengthwise, whereas white matter fractures transversely. Stress applied to produce alternative lines of fracture may not yield a "clean break" and conceivably could result in illusory or ill-defined structures.

Etching techniques have been used in ultrastructure studies of other fossil groups, e.g., brachiopods (Sass, 1967; Williams, 1968) and molluscs (Hudson, 1968). Material removed is undoubtedly selective, but structural patterns are accentuated. We studied sections using progressively extended etching times to observe changes occurring from polished, normal, and fracture surfaces to those intensively etched. Etching is not extreme in most of our work as is indicated by the persistence of fine polishing grooves.

The greatest advantage of our technique, however, is the control of orientation of faces. For each form species examined from each locality, we used at least three embedded specimens to examine longitudinal, transverse, and basal transverse sections. Usually more than three specimens were studied, and oblique lines of sections were commonly made with curved specimens. With many conodonts, including examples of the two genera considered here, we made serial sections to trace structures or to pass from white to hyaline matter. Illusory features and artifacts, which may result with electron microscopy (poor coating for example) are avoided or identified by using numerous specimens and orientations for each form species. The ultimate justification of the techniques used is in the result. In the Panderodontidae, we consider that new information has been provided by our embedding and etching techniques but stress that all methods (etching, fracturing, thin-sectioning) are useful and should be used to complement each other.

To obtain wide geographic and stratigraphic coverage, specimens from several horizons and localities were studied. Specimens of form species that we examined (all not illustrated here) were as follows:

Belodina compressa (Branson and Mehl): Chaumont Formation, Black River Group, Middle Ordovician, upper Ottawa Valley, Ontario, locality 2 of Barnes (1967b); Prosser Member, Galena Formation, Middle Ordovician, east side, Highway 52, south of Decorah, Iowa (locality 3, Ethington, 1959).

B. sp. A: Farr Formation, Upper Ordovician, Shipyards Quarry (47°29'N, 79°39'W), Lake Timiskaming outlier, Ontario (Munro and Barnes, unpublished data).

B. sp. B: Farr Formation, Upper Ordovician, Shipyards Quarry (47°29'N, 79°39'W), Lake Timiskaming outlier, Ontario (Munro and Barnes, unpublished data).

Panderodus arcuatus (Stauffer): Farr Formation, Upper Ordovician, Shipyards Quarry (47°29'N, 79°39'W), Lake Timiskaming outlier, Ontario (Munro and Barnes, unpublished data).

P. compressus (Branson and Mehl), including both *P. compressus* s.s. and the gerontic *P. feulneri* (Glenister): Prosser Member, Galena Formation,

Middle Ordovician, east side, Highway 52, south of Decorah, Iowa (locality 3, Ethington, 1959). Chaumont Formation, Black River Group, Middle Ordovician, upper Ottawa Valley, Ontario, locality 2 of Barnes (1967b).

P. gracilis (Branson and Mehl): Chaumont Formation, Black River Group, Middle Ordovician, upper Ottawa Valley, Ontario, locality 2 of Barnes (1967b); Prosser Member, Galena Formation, Middle Ordovician, east side, Highway 52, south of Decorah, Iowa (locality 3, Ethington, 1959); Farr Formation, Upper Ordovician, Shipyards Quarry (47°29'N, 79°39'W), Lake Timiskaming outlier, Ontario (Munro and Barnes, unpublished data).

P. intermedius (Branson, Mehl, and Branson): Prosser Member, Galena Formation, Middle Ordovician, east side, Highway 52, south of Decorah, Iowa (locality 3, Ethington, 1959).

P. panderi (Stauffer): Farr Formation, Upper Ordovician, Shipyards Quarry (47°29'N, 79°39'W), Lake Timiskaming outlier, Ontario (Munro and Barnes, unpublished data).

P. unicastatus (Branson and Mehl): Crug Limestone, Upper Ordovician, Crug Farm, Llandeilo, Wales (Bergström, 1964).

P. simplex (Branson and Mehl): 15 cm below top of Hamra Group of Munthe (1921) (or within Sundre Beds of Martinsson, 1962), Upper Silurian, Juves, Gotland, Sweden.

P. unicastatus (Branson and Mehl): 15 cm below top of Hamra Group of Munthe (1921) (or within Sundre Beds of Martinsson, 1962), Upper Silurian, Juves, Gotland, Sweden.

Specimens of *P. gracilis* and *B. diminutiva* (Branson and Mehl) were examined with the transmission electron microscope (TEM) (Hitachi-11, Perkin-Elmer Corp., Norwalk, Connecticut), but did not reveal additional information. All specimens are deposited in the Department of Earth Sciences, University of Waterloo, Waterloo, Ontario.

Ultrastructure of Panderodontidae

CRYSTALLITES

Distinct, unequivocal crystallites that comprise the lamellae are only rarely visible. Crystallites that are seen (Figs. 3F,G; 8F) are usually elongate, with a diameter of 0.1–0.2 μm in *Panderodus*, as found also by Lindström and Ziegler (1971, p. 12). In *Panderodus* and *Belodina*, where lamellar surfaces are exposed inside the basal cavity (Figs. 8C,D; 11C,D), crystallites appear to be granular. Possibly their appearance is merely a result of viewing their basal pinacoids, but a trend from linear crystallites in the cusp to granular crystallites in the base has been noted in other conodonts (in *Ptiloconus* by Barnes *et al.*, 1970, and in *Cardiodella* by Barnes, Sass and Monroe, in press).

Crystallites, when elongate, are oriented with the long axes parallel to that of the long axis of the conodont, but orientation in specimens of species of

Belodina was less easily determined. Alignment of the crystallites at an angle of 30° to the interlamellar spaces (Fig. 11D) may represent the laminated pattern that was interpreted by Lindström and Ziegler (1971, p. 13, text-fig. 3) as platy crystallites arranged parallel to prism pair II, that is, to crystallite faces oriented at an angle of 30° to the external surface of the conodont.

LAMELLAE

In specimens of *Belodina* spp., lamellae are distinct in hyaline matter and are either about $0.8\ \mu\text{m}$ thick (Fig. 11F) or $1.2\ \mu\text{m}$ when thickened in curving towards the basal cavity (Fig. 11B). Species of *Panderodus* show two sets of lamellae, one roughly concentric around the basal cavity and a second, referred to here as radial lamellae, normal to the outer surface. Thickness of radial lamellae is about $1.0\ \mu\text{m}$, but increases to $3.0\ \mu\text{m}$ where they curve near their origin close to the basal cavity (Figs. 6B–D, 7C–E). The concentric lamellae are usually thinner, ranging from 0.2 – $0.8\ \mu\text{m}$ in thickness (Figs. 3G; 4B).

INTERLAMELLAR SPACES

In most of our illustrations, lamellae are evident and are separated by interlamellar spaces, usually one-half to one-third the thickness of the lamellae. Such spaces are not so evident on fractured surfaces and doubtless were accentuated by the etching technique. Lindström and Ziegler (1971, p. 12) did not observe interlamellar spaces in Panderodontacea. But lamellae are recognized through the presence of planes of parting or by planes separating them. These planes on fractured surfaces seem to include irregular spaces (Lindström and Ziegler, 1971, pl. 1, fig. 6; pl. 6, figs. 5–7, for example). Lamellae thus probably are partly fused and partly separated by irregular voids, a condition found also in *Drepanodus homocurvatus* by Barnes *et al.* (1970, p. 4).

In *Panderodus* specimens, transverse sections revealed widely-spaced lamellae at various places close to the basal cavity (Figs. 3E, 5C,D,F; 6A,D). These best developed occur where radial lamellae, normal to the outer surface, curve sharply near their point of origin within a few lamellae of the basal cavity. Wide, interlamellar spaces would likely appear as voids in equivalent fractured sections.

WHITE MATTER

The physical properties of white matter found in the tip of specimens of *Panderodus* (Fig. 3A–D) and in denticles and the cusp of specimens of *Belodina* (Fig. 4E–H) do not differ from those described in many genera of cancellate conodonts (Barnes, Sass and Monroe, in press). The transition from lamellar hyaline to porous, finely-crystalline white matter in *Panderodus* is shown in Fig. 4B,D. The more widespread distribution of white matter in *Belodina* is illustrated in Fig. 10A–G. An outer lamellar zone passes inwards through incipient white matter to a core of true white matter. Only the initial core of denticles is lamellar, the remainder being secondarily converted

to white matter. But, this conversion does not destroy the identity of the denticles, which are distinctly defined by sharp planes.

Hyaline conodonts, especially neurodonts, tend to fracture lengthwise, i.e. parallel to the length of the lamellae. White matter, however, usually fractures transversely, often along lines of holes (Barnes, Sass and Monroe, in press). Lindström and Ziegler (1971, p. 16) considered that holes and fine crystallinity reduced the resistance of white matter to mechanical fracturing. They also suggested that these features might be functionally advantageous, in that they would deter a predator by leaving a mass of broken conodont tips in its throat. White matter likely retained some organic matrix, but its actual potential strength, as compared to a hyaline matter, must be conjectural. A predator, moreover, presumably would consume the entire conodont and be undeterred by a few broken tips. The direction of fracturing is the critical factor. In hyaline forms breakage commonly results in a complete longitudinal fracturing and subsequent severance of a cusp or process. Conversely, in white matter the same stress would probably produce a transverse fracture that only removes the cusp or denticle tip(s).

BASAL FILLING

The basal filling is commonly present in specimens of taxa pertaining to the Panderodontidae and may protrude some distance from the basal rim. Its retention is doubtless promoted by the shape of the deep, narrow basal cavity. At high magnifications we could not obtain photomicrographs of good resolution of crystallites of the basal filling but agree with Pietzner *et al.* (1968) and Lindström and Ziegler (1971) that crystallites develop isometrically with a size range of 0.1 to 0.2 μm .

The structure of the basal filling is lamellar (Fig. 9C–G), with the thickness of lamellae similar to that of the hyaline matter. Only rarely were these lamellae seen in contact with and matching lamellae of the hyaline matter (documented for other conodonts by Müller and Nogami, 1971) due primarily to an apparent contraction of the basal filling away from the hyaline matter (Fig. 9A,B). Lindström and Ziegler (1971, text-fig. 5) suggested that the basal filling had a higher proportion of organic matrix than the hyaline matter and was flexible (perhaps analogous to cartilaginous tissue) but suffered post-mortem contraction. Holes, averaging 3–4 μm in diameter, occur in our material (Figs. 5E; 9C,E,F), but lamellae bend around them, suggesting a primary origin. Primary holes, or tunnels, were confirmed by thin-section studies of other genera by Müller and Nogami (1971, text-fig. 15), who considered that some may have been filled by the inward secretion of lamellae. In longitudinal sections, these holes in *Panderodus* species appear to be arranged in rows parallel to the long axis of the conodont element (Fig. 9E).

OUTER ORNAMENTATION

Six types of outer ornamentation of the Panderodontacea were described by Lindström and Ziegler (1971). We agree with and have nothing further to add to their comments concerning smooth surfaces, fine striations, basal

wrinkles, and denticle ornamentation but have additional information regarding striations, the longitudinal furrow, and coarse striations.

Longitudinal Furrow

In *Panderodus* and *Belodina* species a longitudinal furrow or groove is located on the inner side close to the posterior margin and extends virtually the entire length of the element. As was observed also by Lindström and Ziegler (1971), the furrow penetrates almost to the basal cavity as a deep narrow slit in cross-section. The width of the slit on etched sections is about 2–3 μm on the outer surface, narrowing rapidly inwards to 1 μm , and then closing completely within a few microns of the cavity (Figs. 3E; 4A,C,D; 5A,C,D). In cross-section the slit is roughly parallel to the outer lateral face but at its origin usually swings sharply tangential to the basal cavity, near which it is associated with the curved, widely-spaced, radial lamellae (Figs. 3E; 5C,D,F; 6A,C,D). Lindström and Ziegler (1971, fig. 3) demonstrated that the furrow does not reach the tip of the cusp in *Panderodus* and broadens to a shallow, wide groove towards the basal margin. The groove likewise does not reach the tip of the cusp in *Belodina* but continues as a narrow structure to the basal rim. At the rim, the groove produces a constriction in the base that assists in producing the bifid basal cavity of certain species (Figs. 4F,G; 11A,E).

Coarse Striations

The longitudinal furrow is usually flanked by a zone, 3–5 μm wide, that is relatively smooth and lacking in striations (Figs. 3H; 6D). Beyond these smooth zones occur coarse, longitudinal striations or ridges. The ridges, which are the surface expression of the radial lamellae, are readily observed with the light microscope and, when well developed, have even been used as a specific character (e.g., *Panderodus striatus* Stauffer, 1935).

We observed striations in both longitudinal and transverse sections. On the inner, lateral face they extend from the anterolateral shoulder, or carina, almost to the posterior margin. Striations, about 1 μm wide and consistent in width along their length (Fig. 7C–E), are more regular than those of concentric lamellae. From the inner lateral face, they pass inwards to approach the basal cavity. Striations anterior to the longitudinal furrow originate as curved, widely-spaced lamellae adjacent to the cavity referred to previously (Figs. 3E; 5C,D,F). Thus, striations are not merely surface ornamentation that persist through ontogeny as was suggested by Lindström and Ziegler (1971); they represent lamellae that develop normal to the outer surface and are thus radial rather than concentric with reference to the basal cavity. Hence, in conodonts of the family Panderodontacea the method of element construction is radically different from the simple, concentric, lamellar growth of most other conodonts (documented, for example, by Müller and Nogami, 1971).

Radial lamellae intersect the longitudinal furrow at angles of 30° to the anterior side and 15° to the posterior side. They appear to terminate just before reaching the furrow, thus producing a smooth, flanking zone. As axes

of the radial lamellae and the furrow intersect, and as the furrow follows the curve of the element, some striations ultimately overlap and terminate. The anteriormost radial lamella on the inner lateral face extends the most distal toward the tip of the cusp, and others are added at the edge of the furrow farther down its length. As seen in longitudinal sections (Figs. 6B-D; 7C-E) new lamellae develop apically at positions progressively distal from the tip of the cusp. As many as 20 such lamellae occur anterior to the furrow and about 10 posterior to the furrow. Some posterior lamellae terminate as the furrow extends outward during growth.

Striations were interpreted by Lindström and Ziegler (1971, p. 14) as surface ornamentation whose form was controlled primarily by the orientation of crystallite faces. In their illustration (1971, fig. 1) striations penetrate into the element, and hence they interpreted this condition to reflect ontogenetically-persistent ornamentation of the surface. Probably the space between the striations in our sections was produced in part by etching, but distinct planes of separation are also evident in fracture surfaces of material studied by Lindström and Ziegler. Further, if these striations were simply surface ornamentation, concentric lamellae would be expected to transect them and to be evident in the region of the inner, lateral face. But concentric lamellae are absent there. Moreover, as was demonstrated above, striations may be traced inwards as radial lamellae terminating as widely-spaced, curved lamellae built upon the few, initial, concentric lamellae that define the margin of the basal cavity (Figs. 5E,F; 6C,D).

Radial lamellae are especially distinct in hyaline matter (Fig. 7C-E), but are less evident in areas of incipient white matter (Fig. 4A-D). A sharp plane of separation, or suture, might be expected where the concentric lamellae intersect with radial lamellae. A suture should occur inwards from the anterolateral shoulder, or carina, and near the posterior margin. But, other than an indistinct interlamellar space or plane separation, we observed no sharp boundary in this region.

Although coarse striations occur on the outer surface of specimens of *Belodina* spp. (Lindström and Ziegler, 1971) whether these have the same structural basis as those in specimens of *Panderodus* spp. is not known. The longitudinal furrow is certainly deep and narrow (Figs. 10F; 11E), but if flanked by striations representing radial lamellae, they are not evident internally. We consider that the coarse striations illustrated by Lindström and Ziegler (pl. 3., figs. 7, 8) on the anterior margin represent the surface outcroppings of lamellae or crystallite bundles.

FUNCTION OF RADIAL LAMELLAE AND THE LONGITUDINAL FURROW

Radial lamellae on the inner lateral face are primary lamellae flanking the longitudinal furrow and are distinct from the concentric lamellae. With formation of concentric lamellae, the outer part of the element must have been covered by a secretory tissue producing an organic matrix that was mineralized by linear, apatite crystallites. With radial lamellae, it would appear that lines of secretory cells must have been present on the edges of the lamellae at the outer surface. The rows of cells gradually retreated outward with growth

while retaining their linear form and parallelism. No rhythmic secretion is apparent within each radial lamella as it extended outwards.

Lindström and Ziegler (1971) suggested the longitudinal furrow to be a possible site for the insertion of muscles termed *retractores tentaculorum*. Certainly the furrow is a prominent and characteristic feature of the *Panderodontidae* and likely to have been functionally important. Few conodonts display such deep invaginations into their elements, and these furrows may well have been impossible to produce unless radial lamellae were adopted. The furrow must have been occupied by tissue during its growth, but we cannot prove that the tissues remained after the element was complete. In *Panderodus* spp. at least, additional, final lamellae were only secreted in the basal region (Fig. 1) and may represent a basal withdrawal of secretory tissue. Certainly a theory of muscle insertion seems equally probable to an alternative hypothesis that the furrow developed on elements functioning as exposed masticators. But the ultrastructure of all major conodont groups needs to be investigated before an hypothesis of the function of conodont elements can be realistically proposed.

MODE OF GROWTH

After an examination of numerous specimens along many different planes of section, the mode of growth can be described for *Panderodus* and *Belodina*. Figs. 1 and 2 were assembled from illustrations given here and from others not reproduced in this paper.

Panderodus

A few, initial, concentric lamellae were secreted, outer ones progressively overlapping inner ones, to provide a downward extension and progressive deepening of the basal cavity. The longitudinal furrow was then initiated on the inner lateral side in a direction almost tangential to the basal cavity wall but not intersecting it. Anterior to this furrow a group of new, radial lamellae originated. They arose at a high angle; some vertical to the outermost initial lamella were widely spaced proximally, then curved sharply to become radial in orientation. New radial lamellae originated at the anterior tip of the furrow, with subsequent ones added progressively lower down the length of the furrow. Others were terminated by extension of the furrow, with growth over those to the posterior. The anteriormost radial lamella is thus the oldest and apically overlaps the next, which is younger. At this stage of growth two sets of lamellae were present: (a) radial lamellae on each side of the longitudinal furrow, restricted to the inner lateral face between the anterolateral shoulder or carina and near the posterior margin, and (b) thinner, concentric lamellae passing from the anterolateral shoulder around the outer lateral face to the posterior margin or just beyond. Concentric lamellae were added externally, extending progressively farther basally. They also appear to extend over the tip of the cusp, but extension of the element is limited apically, and most of the increase in length was basal.

As the middle phase of growth continued, hyaline lamellar matter was transformed, secondarily via incipient white matter, to white matter at or

above the basal cavity tip. White matter spread outward to ultimately occupy all the entire tip, save for a few outermost lamellae. White matter may also be found in small, isolated pods along the posterior margin, especially where germ or proper denticles developed in certain panderodids.

The end of the middle growth phase is defined as the time at which maximum length was achieved. The longitudinal furrow had widened from a narrow, deep slit to a broad, shallow groove. Radial lamellae usually terminated before reaching the basal margin, apparently overlapped by concentric lamellae that did not extend far up the element. Restricted, concentric lamellae may indicate an eruption of the main part of the element through the secretory tissue.

In the final growth stage only minor modifications to the element occurred, all appearing at the basal rim. Secretion of concentric lamellae (e.g., Figs. 5E; 8A,C) continued only on the basal part, becoming first well-defined, basal wrinkles (Lindström and Ziegler, 1971) and eventually a distinctly raised rim, about 100 μm wide. These basally-restricted lamellae curve inward toward the basal cavity but disappear on the outer surface as a tangential feather edge. Thus, circular banding is not evident; the linear crystallite bundles, which are unequally developed and comprise the lamellae, produced the basal wrinkles. Expansion of white matter may have continued during this final growth phase.

The above sequence is based on panderodids that we studied and could apply to closely related species. Some species of Devonian panderodids may have had a different growth pattern. Lindström and Ziegler (1971) described the structure of *Neopanderodus perlineatus* (Ziegler and Lindström), which exhibits extremely coarse striations on the posteriolateral faces that also flank a deep, narrow, longitudinal furrow. Whether these, too, represent a form of radial or semicircular lamellae cannot be judged from their illustrations. Unfortunately, the only transverse section (fig. 7D) given by them is from an area near the tip, entirely in white matter, and with the original internal structure lacking.

Belodina

Fewer species and specimens of *Belodina* were examined than for *Panderodus* spp. *Belodina*, being denticulate, is more complex, and the lamellar pattern, largely destroyed by the formation of white matter, is more complicated than in specimens of *Panderodus* spp. Thus, our remarks on the mode of growth of *Belodina* are tentative.

As in *Panderodus* spp., the initial growth phase is defined as the secretion of the first few lamellae that created the form of the tip of the basal cavity. The shape of the lamellae is similar to those in *Panderodus*. The middle stage of growth included the development of the deep, narrow longitudinal furrow. Striations flank the furrow, especially between the furrow and the denticles, but whether they are homologous to the radial lamellae of *Panderodus* spp. is not known. Concentric lamellar growth extended the element only a limited distance basally and, in some species, a bifid cavity is produced. Most growth, however, was posteriorly, developing a denticle series

and heel, and apically, extending the curve of the main cusp.

Denticles originated as small cores of lamellae and, although confluent, are sharply set off from each other by sutures. As they grew posteriorly, their lower parts are covered by lamellae secreted externally on the sides of the element. New denticles were usually added apically by outgrowths from the posterior margin of the main cusp (Figs. 4E–H; 10A). In some species, one or two denticles may have originated from the heel, as this is extended posteriorly and basally.

We wished to determine whether all lamellae constructing the cusp extended over most of the element or whether they were limited. Unfortunately we were unable to study specimens sufficiently devoid of white matter to adequately demonstrate the true, lamellar pattern. A similar difficulty arises with the prominent striations on the anterior margin (e.g., Lindström and Ziegler, 1971, pl. 3, fig. 7) that intersect the margin at an angle of about 30°, are as wide as 6 μm , with some overlapping. Lindström and Ziegler (1971, p. 14) offered a partial explanation of the striations in terms of the prism shape of the apatite crystallites. Our studies are not conclusive. The striations may possibly represent the outcropping of lamellae that do not extend completely along the anterior margin. Lamellae below the lower basal cavity of the belodinid illustrated in Fig. 11A appear to extend from the cavity to intersect the anterior margin rather than to be parallel to the margin. Alternatively, the area just above the tip of that same cavity reveals the broad, inner surfaces of individual lamellae, and an interdigitating pattern is visible. This pattern, presumably of crystallite bundles, is similar to that found on the outer anterior margin.

In the final growth stage of *Belodina* spp. length did not increase, but a raised basal rim that usually lacks basal wrinkles developed as in *Panderodus* spp.

Summary

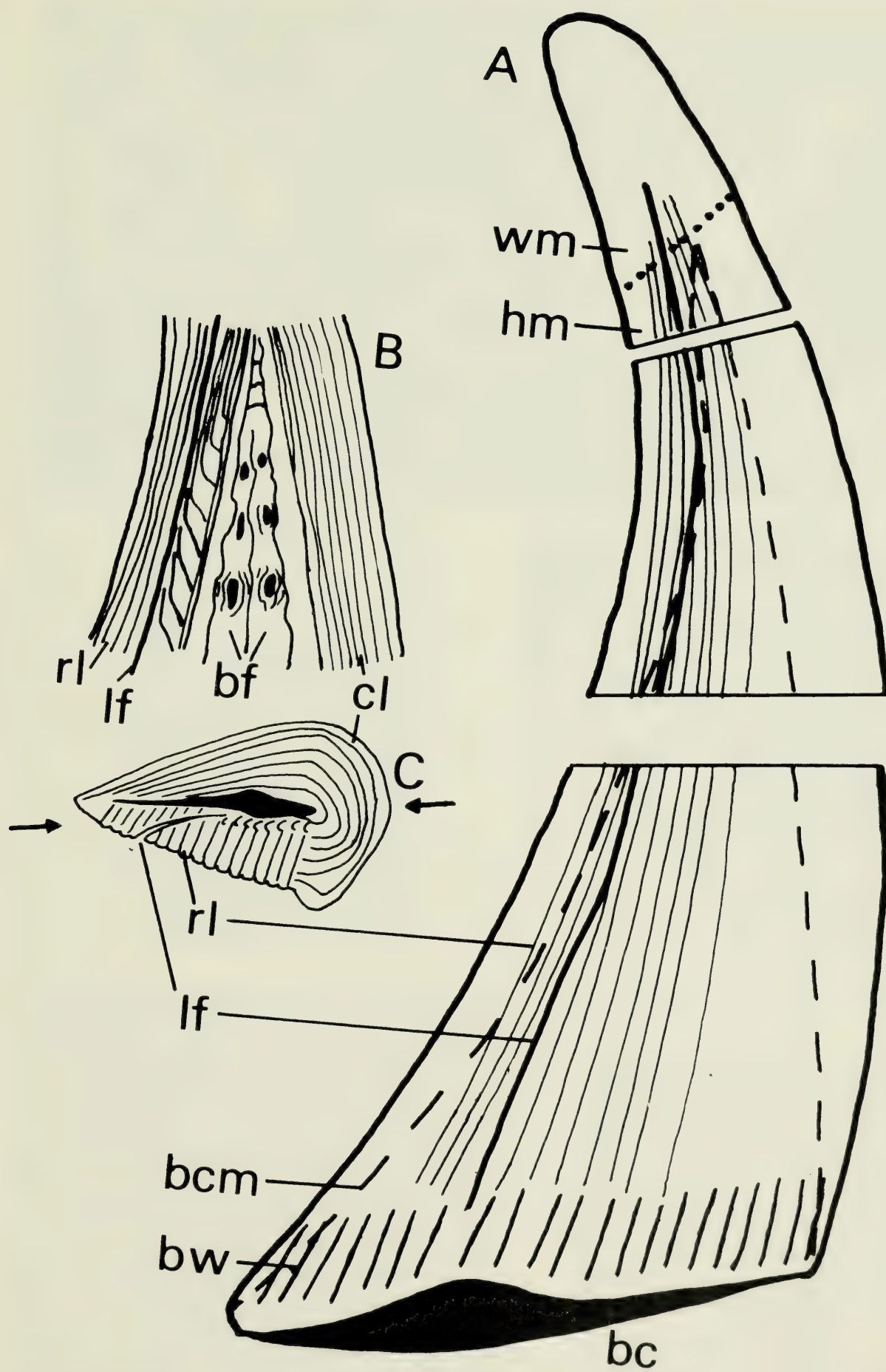
Several methods of ultrastructure investigation of conodonts are necessary and complementary, and the primary technique of etching oriented, polished sections is one that yields the most information. Size and orientation of crystallites in specimens belonging to species of Panderodontidae agree generally with data given by Lindström and Ziegler (1971). However, not only are concentric lamellae present, but the coarse striations found on the surface by Lindström and Ziegler (1971) are shown to be radial lamellae that outcrop on both sides of the longitudinal furrow on the inner, lateral face. They represent a radical departure in element growth in comparison to other conodonts in which only concentric lamellae exist. Known radial lamellae, however, are suspected in other simple-cone genera that possess coarse, surface striations. White matter fractures transversely rather than longitudinally, which is considered functionally advantageous in minimizing damage to the entire element by restriction to the tip of the cusp. The structure of the basal filling suggests a post-mortem shrinkage of mineralized tissue that contained a high proportion of organic matrix. But holes in the basal filling, similar in size and apparently axially oriented, are probably primary. Lamellae of the

basal rim are restricted to that area and do not extend the entire length of the element. A contraction of the secretory tissue to the basal rim is suggested, with a possible eruption of most of the element. Whether tissue, possibly muscles, remained in the longitudinal furrow during the life of the conodont, is open to question. The similarity in ultrastructure of *Panderodus* and *Belodina* further supports the family Panderodontidae as a natural taxonomic unit.

Acknowledgments

C. R. Barnes gratefully acknowledges the continuing financial support of the National Research Council of Canada for conodont research. Support for the research of D. B. Sass was provided by the Alfred University Research Foundation. Miss Carol Frazier kindly assisted in the preparation of the embedded specimens, and we are indebted to R. L. Ethington of the University of Missouri, H. L. Jeppson of the University of Lund and I. Munro of the University of Waterloo for the donation of some of the specimens studied. The research was facilitated by use of the scanning electron microscope at the University of Waterloo and the transmission electron microscope at Alfred University.

Fig. 1—Diagram of a panderodid, *Panderodus compressus*, to illustrate external and internal structure. A) inner lateral view; B) longitudinal section (along axis indicated by arrows in C) of the middle part of the element marked by breaks; C) transverse section of the element at a point marked by lower break. Abbreviations: bc, basal cavity; bcm, basal cavity margin; bf, basal filling; bw, basal wrinkles; cl, concentric lamellae; hm, hyaline matter; lf, longitudinal furrow; rl, radial lamellae; wm, white matter; about $\times 250$.



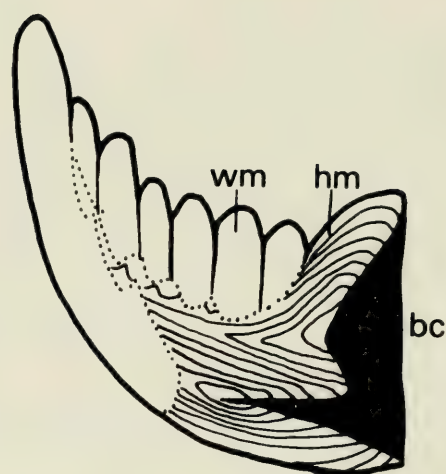


Fig. 2—Diagram of the internal structure of a belodinid, *Belodina compressa*; longitudinal section. Abbreviations in Fig. 1; about $\times 125$.

Fig 3 A-D—*Panderodus gracilis*, a multi-element species comprising the form species *P. compressus* (A,B, inner and outer lateral views) and *P. gracilis* (C,D, inner and outer lateral views). Specimens uncoated and unretouched to show extent of basal cavity and white matter in tip. Bobcaygeon Formation, Middle Ordovician, Great Cloche Island, Manitoulin, Ontario, $\times 80$.

E-G—*Panderodus arcuatus*. Scanning electron (SEM) micrographs of a transverse section near midlength. E) general view. Note radial lamellae flanking longitudinal furrow, both penetrating inwards from inner lateral face; concentric lamellae in remainder of specimen. $\times 290$. F) detail of radial lamellae at outer surface of inner lateral face that penetrate inwards. Small, needle-like crystallites aligned vertical to the plane of section, $\times 5,750$. G) detail of concentric lamellae around anterior part of basal cavity. Note lateral changes in thickness of lamellae; crystallites linearly arranged parallel to the axis of the element; overlapping of lamellae on wall of basal cavity; wide interlamellar spaces immediately anterior to the basal cavity, $\times 1,175$.

H—Detail of striations (radial lamellae) and longitudinal furrow on inner lateral face of *Panderodus gracilis*. Note smooth zones on either side of furrow beyond which are parallel striations extending to anterior shoulder (right) and close to posterior margin (left). Disregard transverse fracture and secondary surface overgrowth. Chaumont Formation, Middle Ordovician, Upper Ottawa Valley, Ontario, $\times 575$.

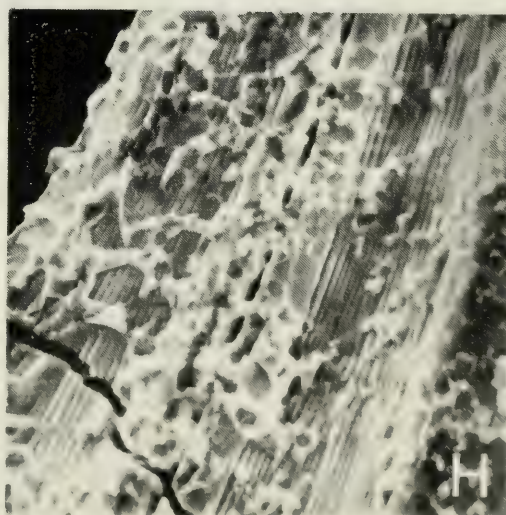
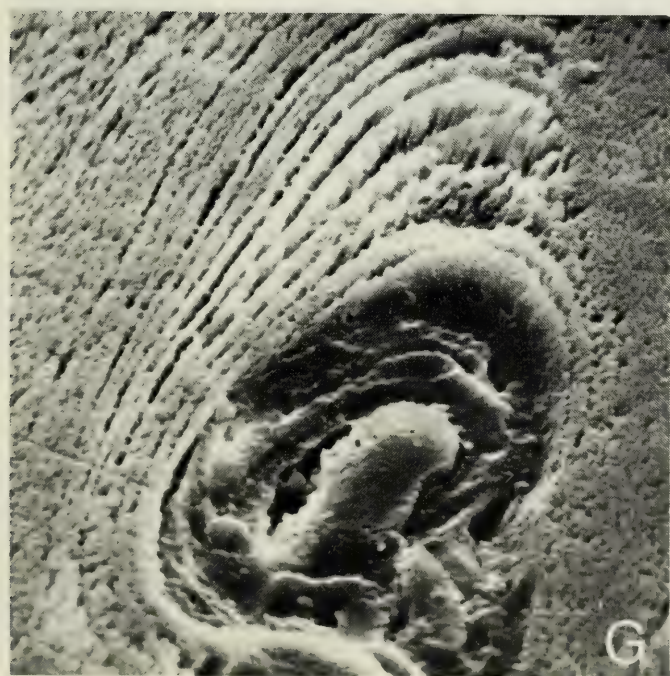
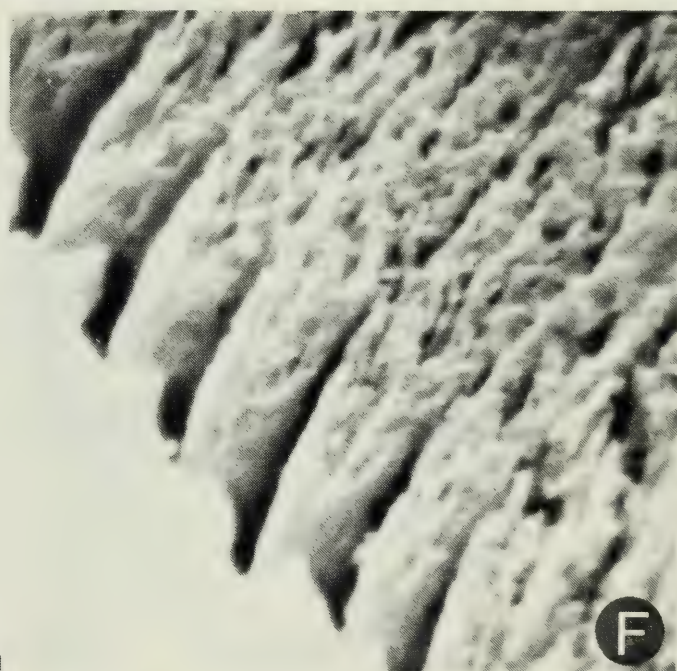
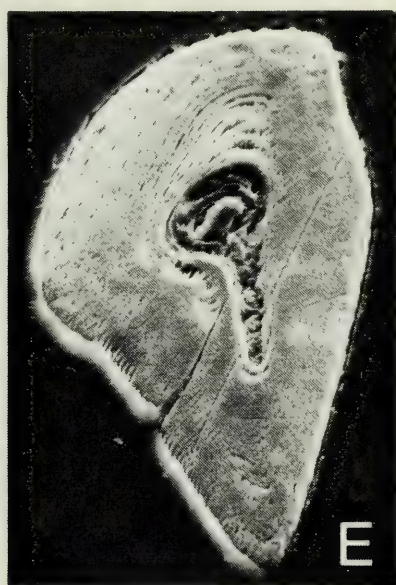
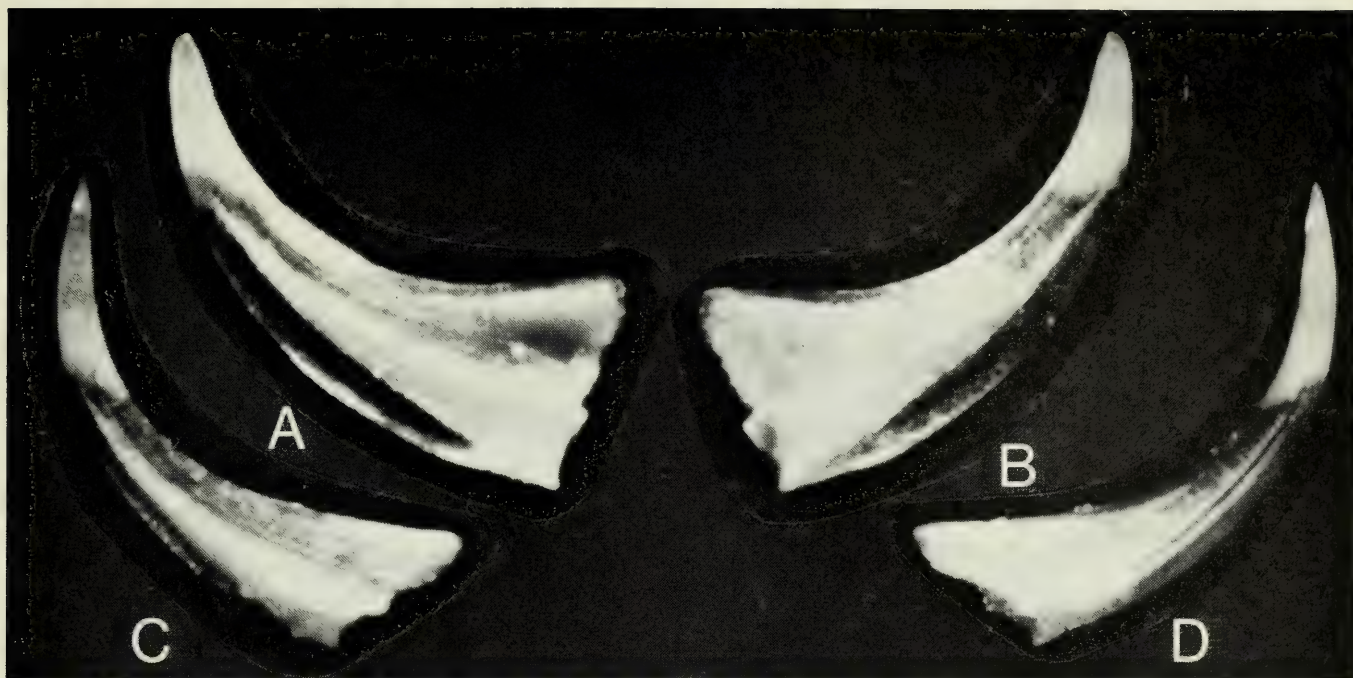


Fig. 4 A-D—*Panderodus compressus*. SEM micrographs of transverse section just below tip of basal cavity. Farr Formation, Upper Ordovician, Lake Timiskaming outlier, Ontario. A) general view. Note small tip of basal cavity; longitudinal furrow penetrating to cavity area, flanked by striations (radial lamellae) on inner lateral face; thinner concentric lamellae throughout remainder of section; darker areas in posterior part representing the lower extensions of white matter, $\times 550$. B) detail on inner lateral face as in Fig. 1. Note longitudinal furrow extending inwards (to upper left) as a narrow slit. Radial lamellae posteriorly (below) intersect furrow region at 15° , whereas those anteriorly (above) intersect at 30° . Mostly incipient white matter, $\times 2,750$. C) detail of posterior region, specimen rotated 90° . Note longitudinal furrow; radial lamellae posterior to furrow; concentric lamellae on outer lateral face; white matter in centre, $\times 1,100$. D) detail as in Fig. 1, close to outer lateral face near posterior margin. Note transition from lamellar, hyaline matter at margin (lower left) to porous, white matter inside (upper right), $\times 2,750$.

E-H—Belodinid components of the multi-element species *Belodina compressa*: *B. compressus* (E,F, outer and inner lateral views) and *B. grandis* (G,H, inner and outer lateral views). Bobcaygeon Formation, Middle Ordovician, Great Cloche Island, Manitoulin, Ontario, $\times 80$.

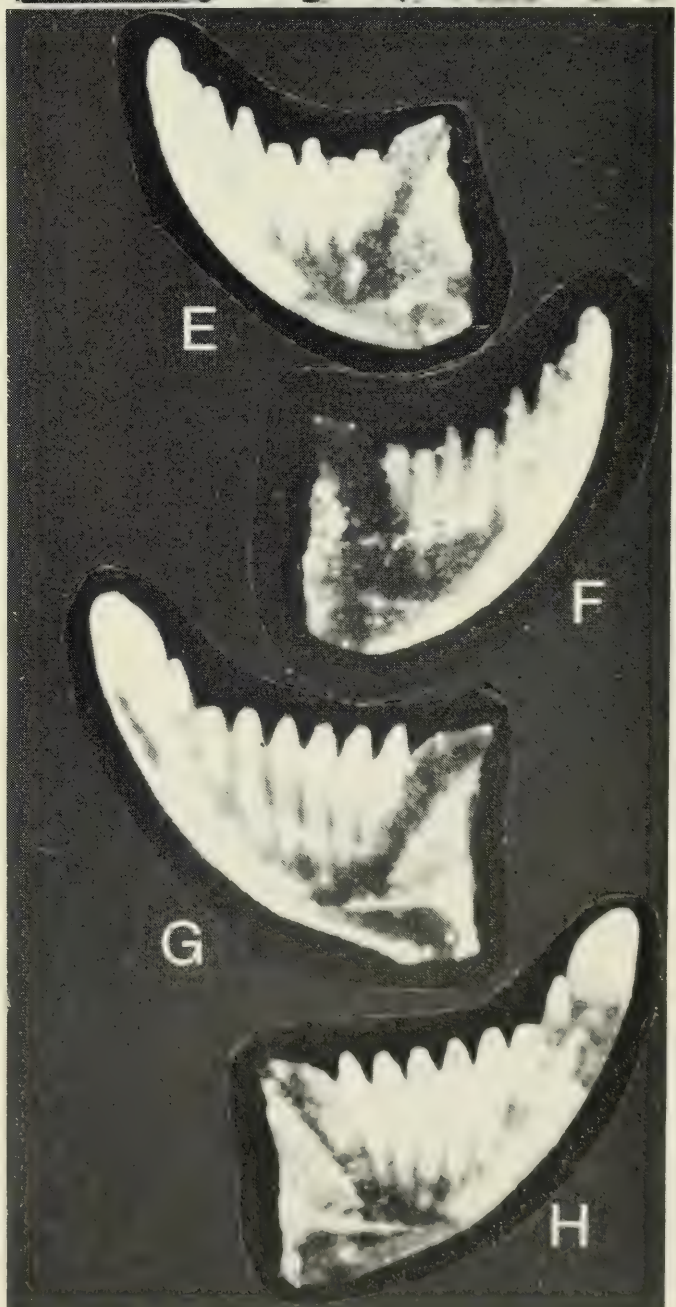
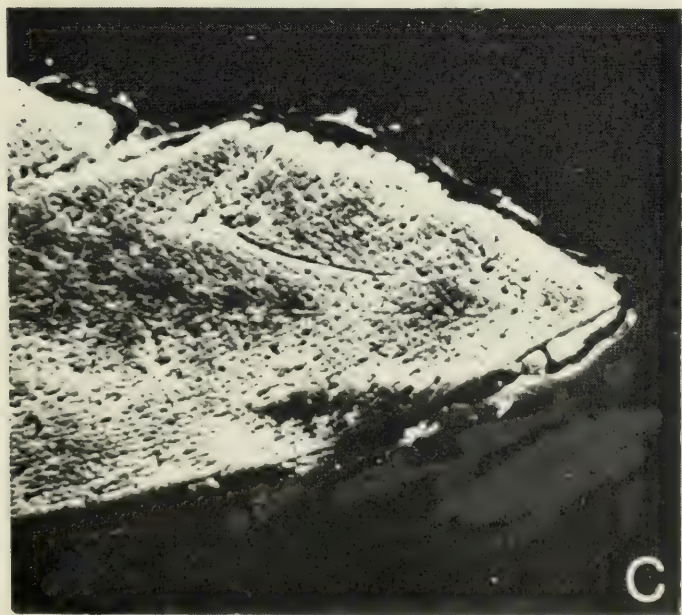
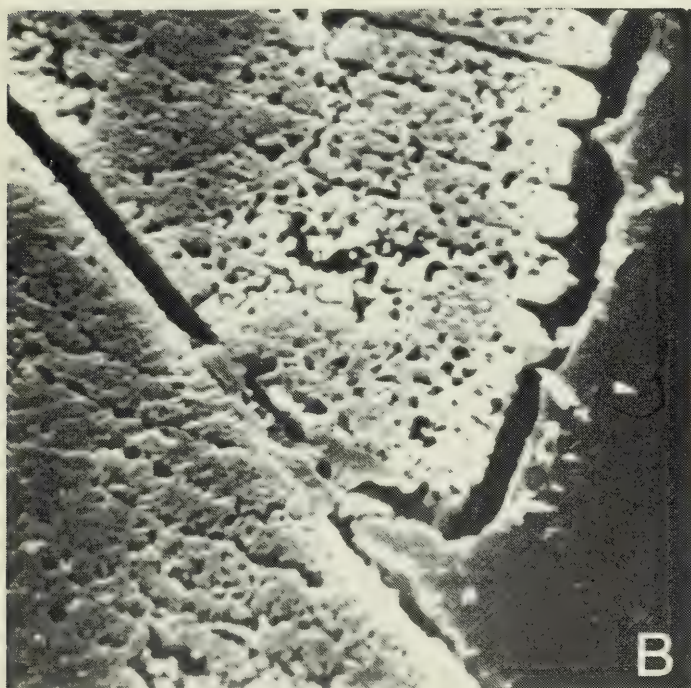
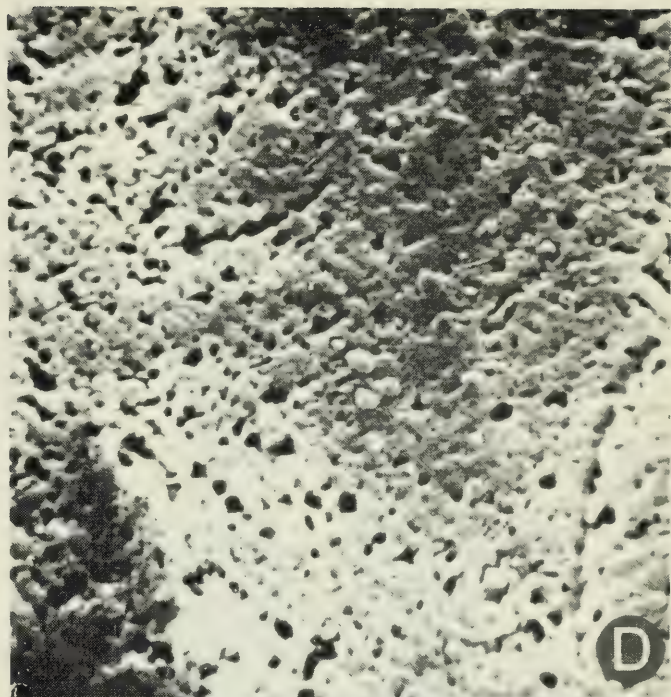
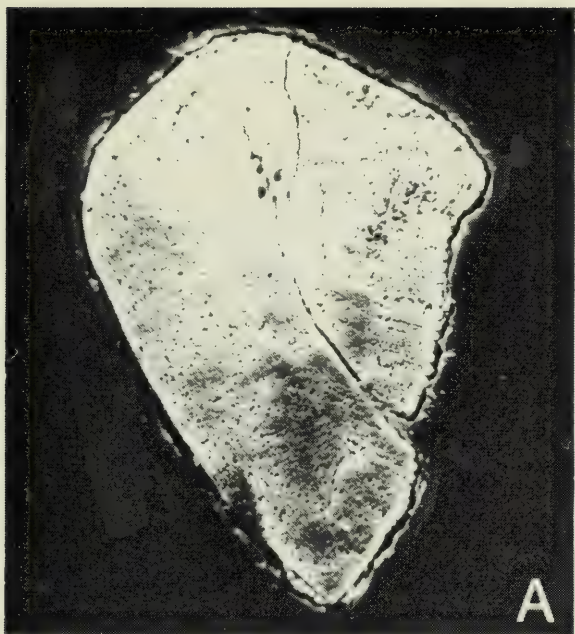


Fig. 5 A-E—*Panderodus compressus*. Farr Formation, Upper Ordovician, Lake Timiskaming outlier, Ontario. A) general view of oblique section through the basal region and cavity just below mid-length, $\times 120$. B) Sketch to show orientation of section shown in Fig. 5A. C) detail of anterior margin and basal cavity. Note overlapping of lamellae in basal cavity; radial lamellae extending from inner lateral face (right) and passing into curved, widely-spaced lamellae just lateral to the basal cavity; longitudinal furrow terminating inside of curved lamellae, $\times 575$. D) detail of lower part of Fig. 5C to illustrate radial lamellae on both sides of longitudinal furrow. Thinner concentric lamellae to left of cavity, $\times 1,175$. E) detail of basal region. Note distinct lamellae that appear to terminate at the outer margin of the basal region; basal filling containing circular holes, $\times 575$.

F—*Panderodus arcuatus*. Section more proximal through same specimen shown in Fig. 3E and rotated 180° . Detail of lamellae anterior to furrow. Note abrupt transition from curved to radial lamellae, $\times 1,200$.

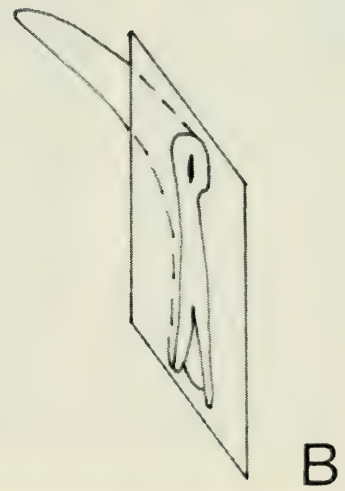
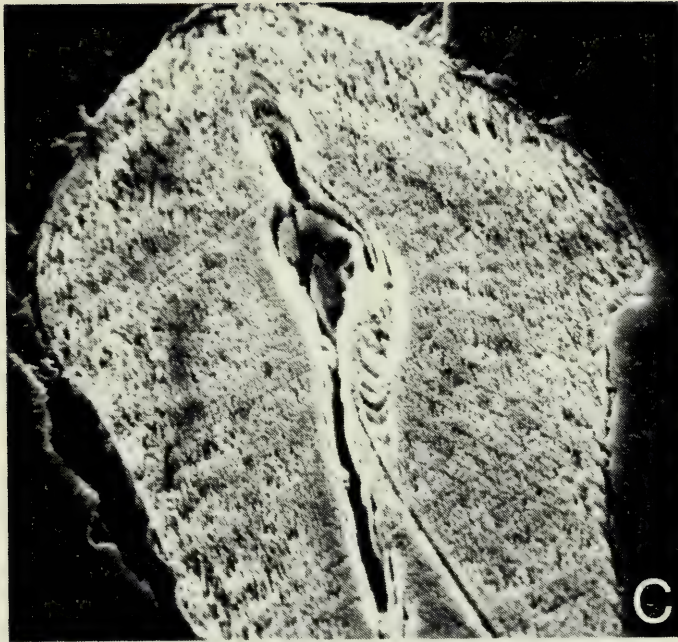


Fig. 6 A-D—SEM micrographs of longitudinal section through *Panderodus arcuatus*. Farr Formation, Upper Ordovician; Lake Timiskaming outlier, Ontario. A) general view of longitudinal section, $\times 165$. B) detail of upper part of section. Note prominent longitudinal furrow with radial lamellae, nearly parallel, on both sides, $\times 1,100$. C) detail of longitudinal furrow, flanked by radial lamellae, some of which overlap lengthwise. Anterior (left) third of section is composed of concentric lamellae, but lamellae not distinct because of oblique intersection with plane of section; separated from radial lamellae by a poorly-defined, almost vertical parting, $\times 550$. D) detail of area proximal to region shown in Fig. 6C, around basal cavity. On anterior (left) side of basal cavity concentric lamellae end as overlapping sheets; on posterior (right) side of cavity, radial lamellae terminate as sharply curved, widely separated lamellae, built upon concentric lamellae defining the wall of the cavity, $\times 1,100$.

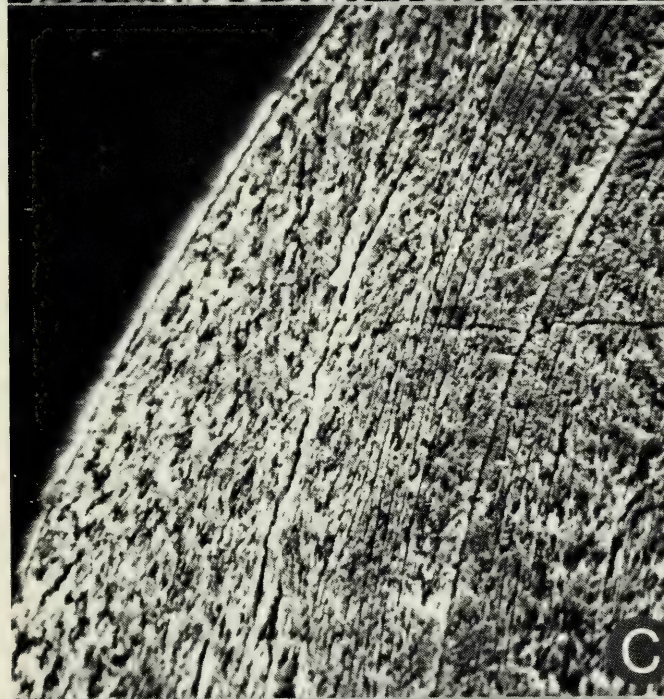
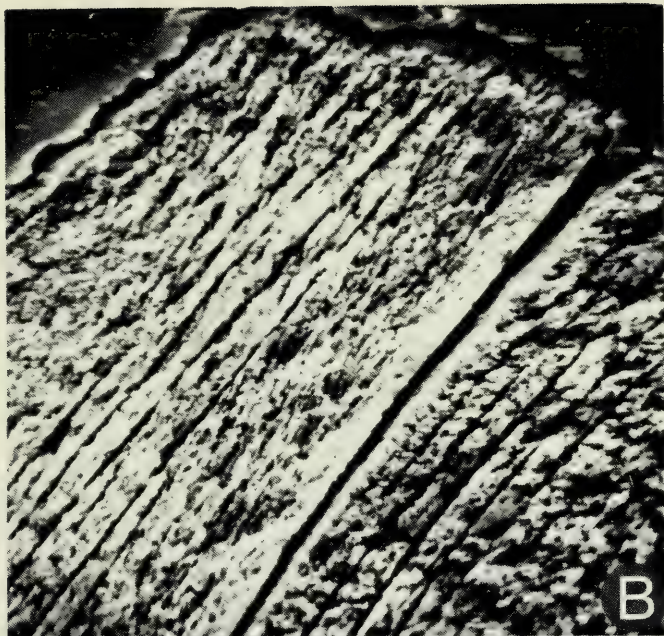


Fig. 7 A-E—SEM micrographs of longitudinal section through *Panderodus compressus*. Farr Formation, Middle Ordovician, Lake Timiskaming outlier, Ontario. A) general view of longitudinal section, with the depressed central part of the inner lateral face largely unexposed, $\times 110$. B) sketch to show orientation of longitudinal section given in Fig. 7A. C) detail of central area of Fig. 7A. Radial lamellae in centre and extreme right; note that several overlap distally. The longitudinal furrow (arrow) is flanked immediately by non-laminated zones, $\times 550$. D) detail of central part of Fig. 7C. Radial lamellae, arrow marks where one lamella overlaps another, $\times 2,750$. E) detail of central part of Fig. 7D. Interlamellar partings, or spaces, well developed; crystallites not apparent within the lamellae, $\times 5,500$.

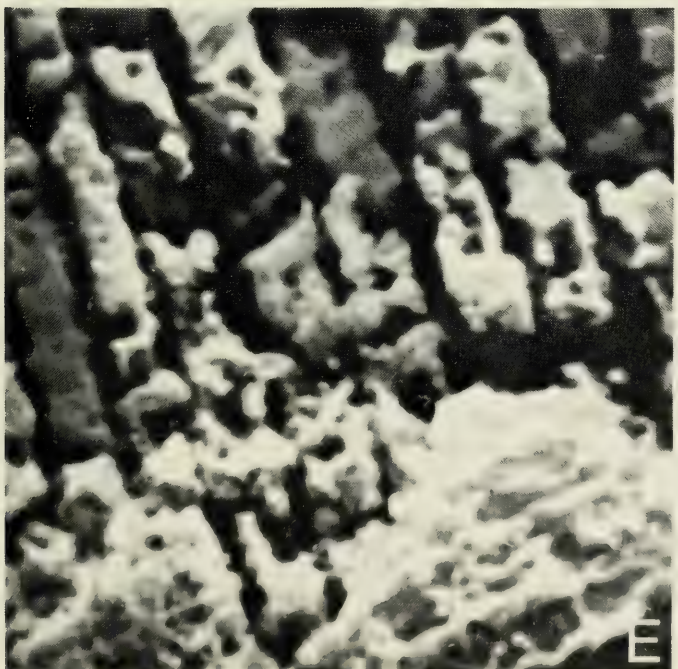
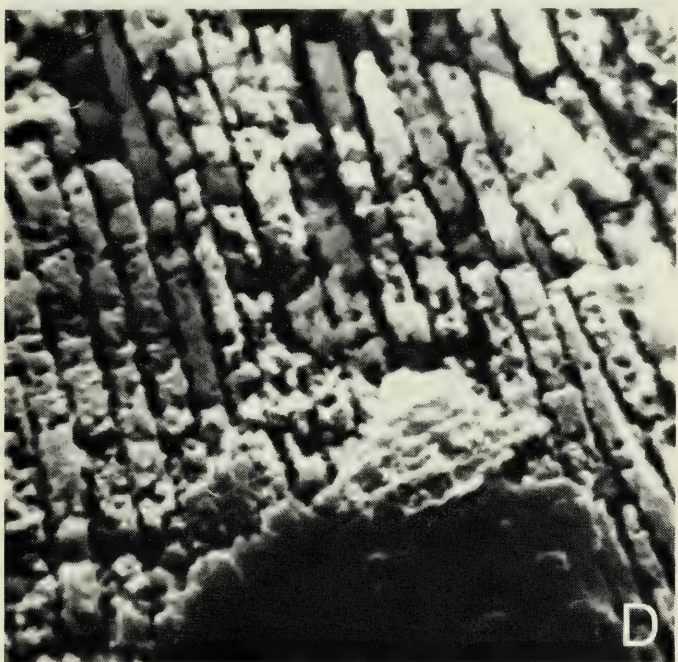
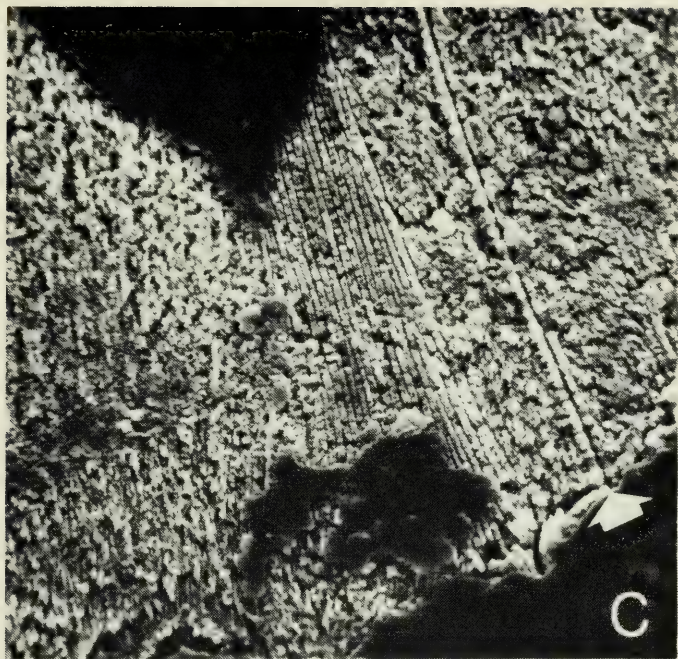


Fig. 8 A-D—SEM micrographs of longitudinal section through *Panderodus compressus*. Farr Formation, Upper Ordovician, Lake Timiskaming outlier, Ontario. A) general view. White matter in tip, inside of inner lateral face exposed in lower part of element, $\times 65$. B) widely spaced, thickened lamellae on anterior side of basal cavity. Compare with transverse section in Fig. 3G, $\times 1,300$. C) overlapping of lamellae that form inner lateral face. Note that lamellae on left would terminate at the outer edge of element and not extend over the cusp tip. Lamellae on right are more numerous and unconformable with those on the left, separated by the lower extension of the longitudinal furrow, $\times 325$. D) detail of centre of Fig. 8C. Note unconformity between two sets of lamellae; crystallites of lamellae are granular, $\times 1,300$.

E-F—SEM micrographs of longitudinal section of *Panderodus panderi*. Farr Formation, Middle Ordovician, Lake Timiskaming outlier, Ontario. E) general view of lamellae intersecting with basal cavity (lower left), $\times 585$. F) detail of centre of Fig. 8E, showing linear crystallites of lamellae arranged parallel to the axis of the element, $\times 5,850$.

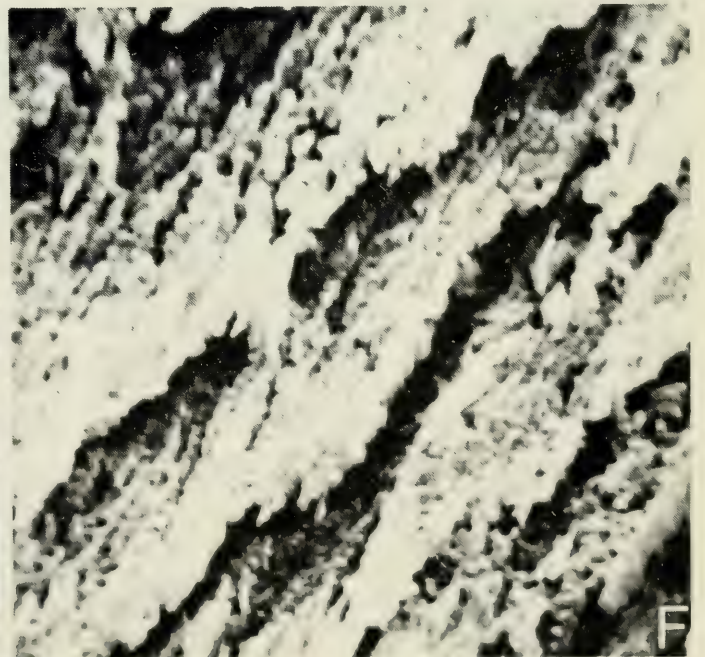
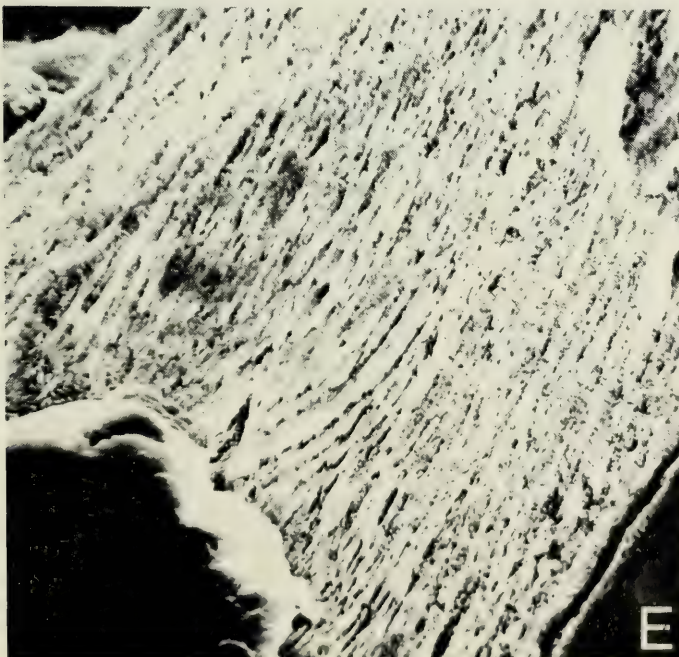
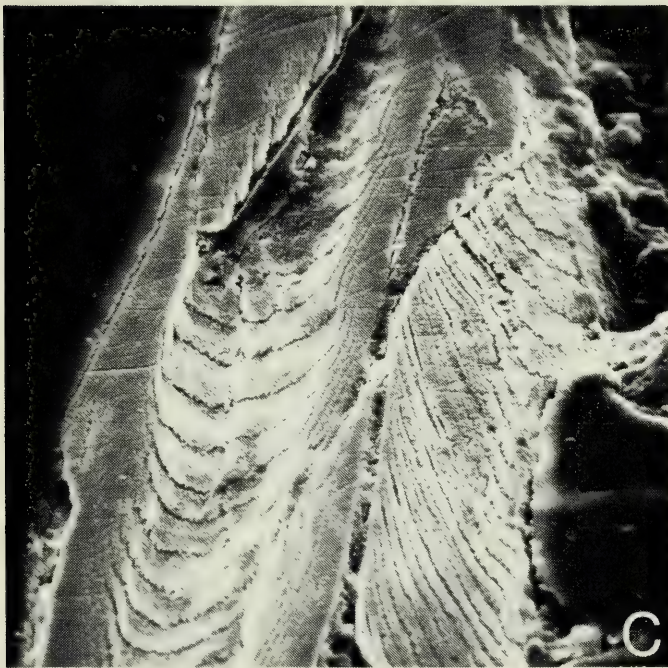
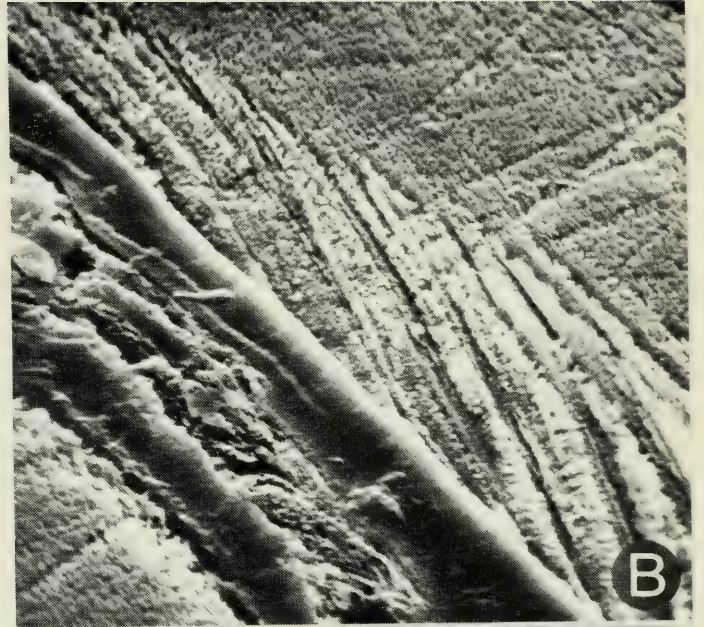


Fig. 9 A-F—SEM micrographs of basal fillings along longitudinal sections of *Panderodus compressus* (*feulneri* type) (C-F) and *Panderodus gracilis* (A-B). From Farr Formation, Upper Ordovician, Lake Timiskaming outlier, Ontario, and Prosser Member, Galena Formation, Middle Ordovician, Decorah, Iowa, respectively. A-B) views of basal filling lower and higher in the cavity, respectively. Note lamellar structure of adjacent hyaline matter (anterior margin to left); overlapping of lamellae down cavity wall; inward contraction of basal filling from hyaline matter. Fig. 9A $\times 570$; Fig. 9B $\times 1,140$. C) general view. Smooth dark areas represent plastic embedding medium. Internal structure is complicated by contraction of basal filling. Lamellae visible in places (lower right), $\times 285$. D) detail of lower right part of Fig. 9C to illustrate lamellar structure of basal filling, $\times 570$. E) detail of basal filling in area proximal to that of Fig. 9D. Note lamellar structure and a vertical row of circular holes, $\times 1,140$. F) detail of hole, with surrounding lamellae shown just above centre of Fig. 9E. Hole is hemispherical and does not represent surface expression of a linear channel, $\times 5,700$.

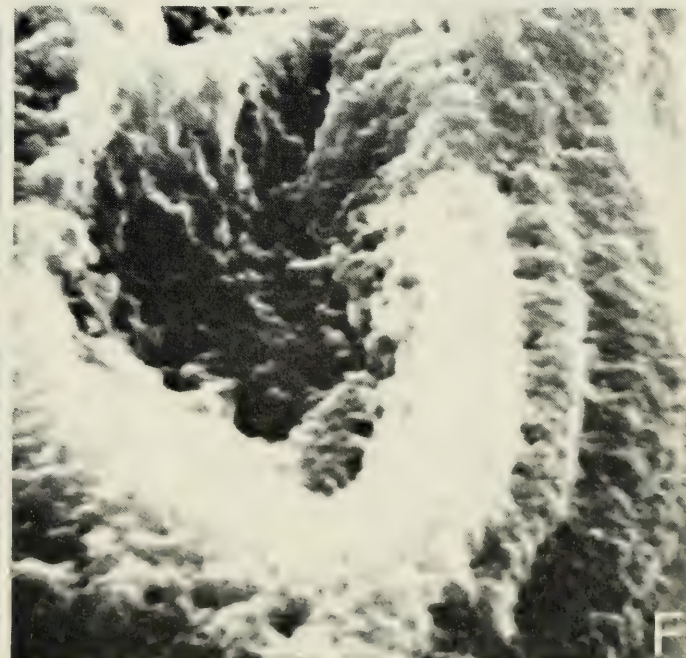
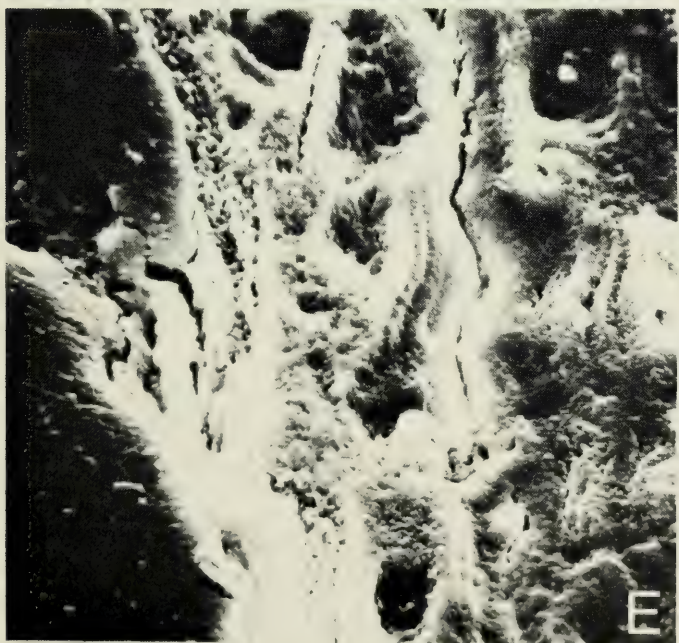
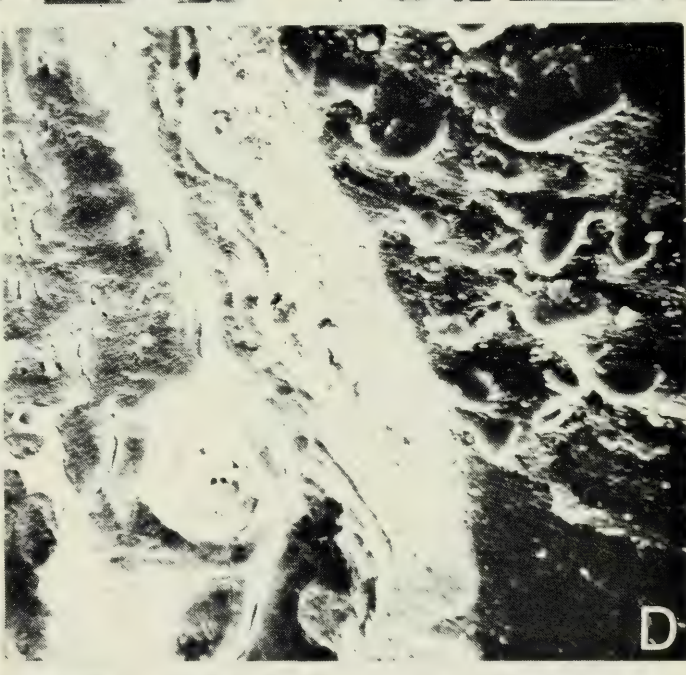
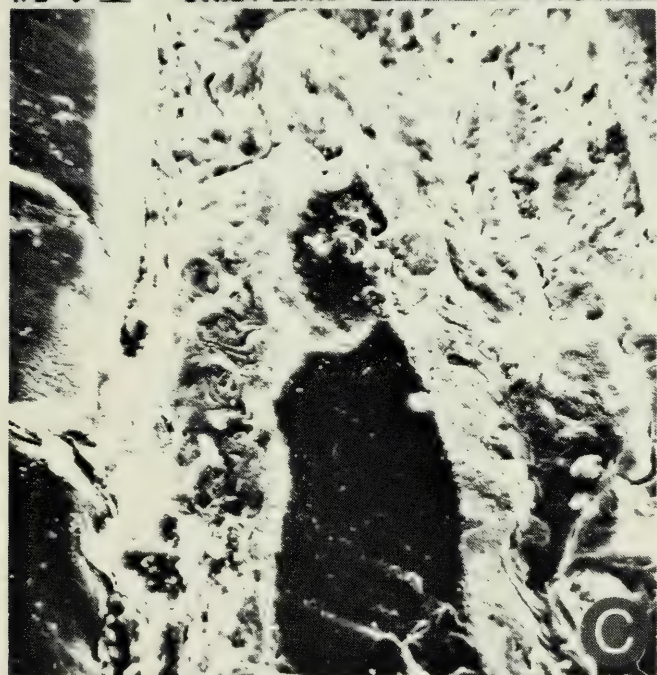
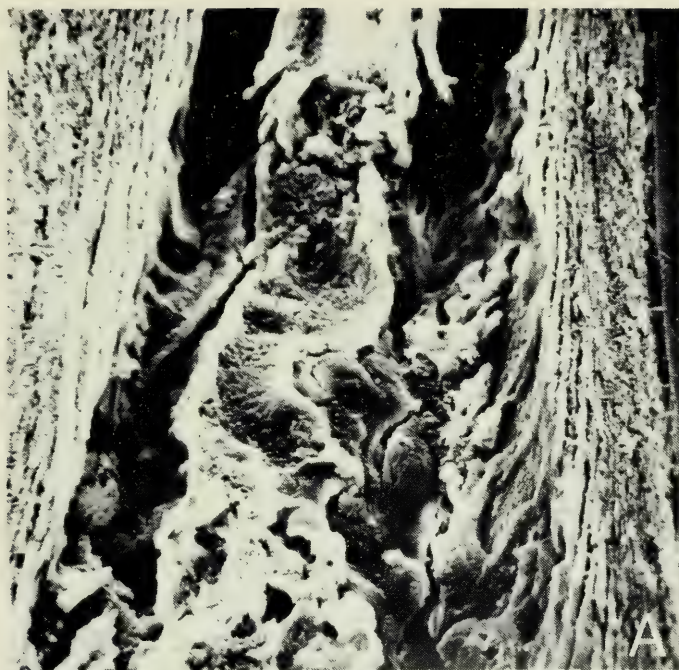


Fig. 10 A—SEM micrograph of weakly etched outer surface of *Belodina* sp. cf. *B. inclinata*. Chaumont Formation, Middle Ordovician, Watertown, New York. Note linear striations at lower left that pass into white matter (light) with small holes and transverse linear voids; main cusp bulbous along its posterior edge as new denticles are being formed within, $\times 480$.

B—G—*Belodina compressa*. Chaumont Formation, Middle Ordovician, Upper Ottawa Valley, Ontario. Three specimens. B) general view of longitudinal section, $\times 110$. C) detail of central part of Fig. 10B. Note section cuts through three denticles, which are clearly defined by near-vertical planes of separation (arrows); each denticle has a lower cone of concentric lamellae that is transformed distally into white matter, $\times 520$. D) detail of cusp from Fig. 10B. Note lamellae along anterior margin passing into a core of white matter; new denticles defined by planes of separation (arrows) developing immediately posterior of core of the cusp, $\times 520$. E) general view of longitudinal section through the base of denticle series (heel at bottom), $\times 265$. F) detail of central part shown in Fig. 10E. Note that section is through three denticles; each has a central crude concentric pattern of the cone of lamellae (open arrow) with white matter beyond (see Fig. 10C); lamellae on extreme (left) outer surface are separated from the denticles by the longitudinal furrow (closed arrow), $\times 1,050$. G) detail of white matter in a denticle along longitudinal section similar to that shown in Fig. 10E but slightly more distal (see Fig. 10C). White matter shows no crystalline structure at this magnification but has both circular and irregular linear voids, $\times 6,000$.

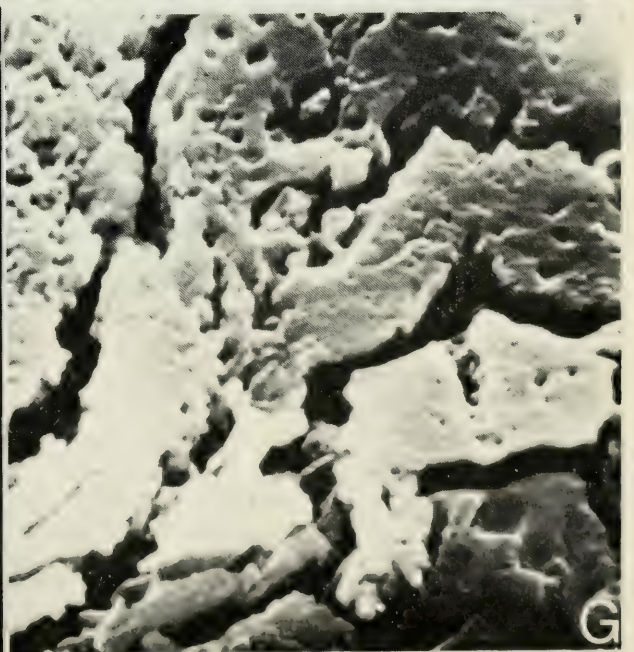
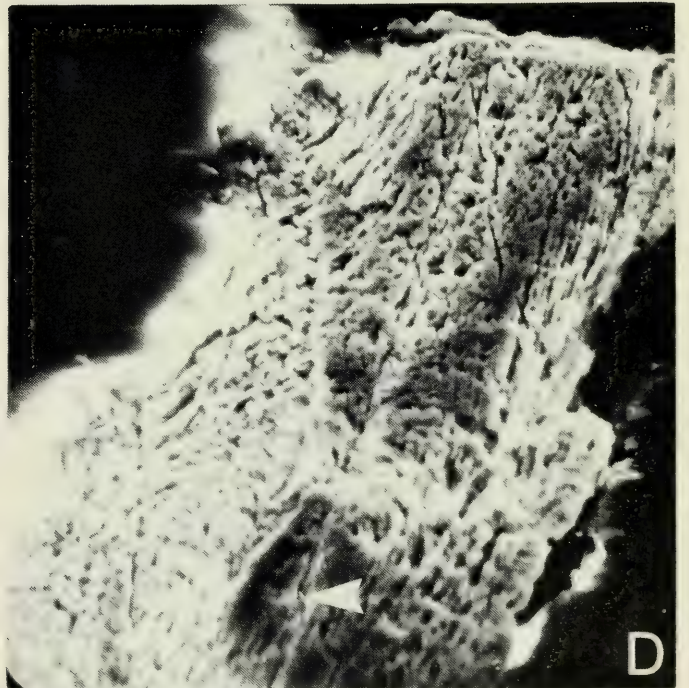
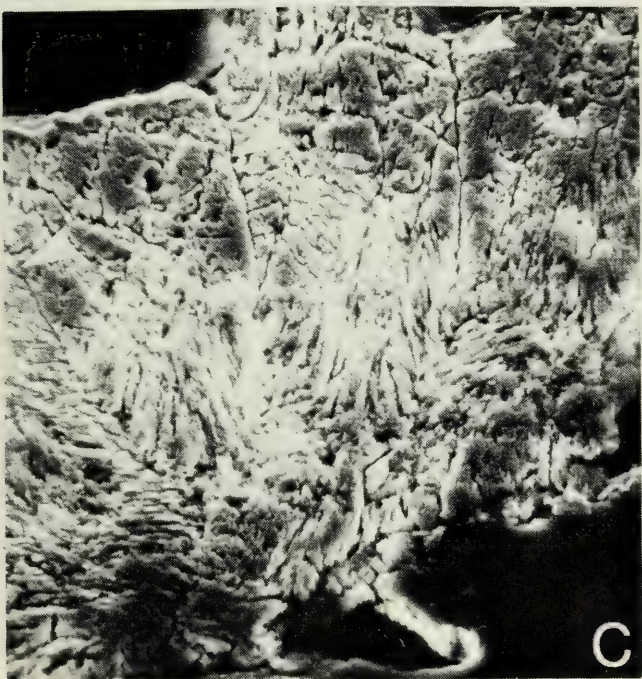
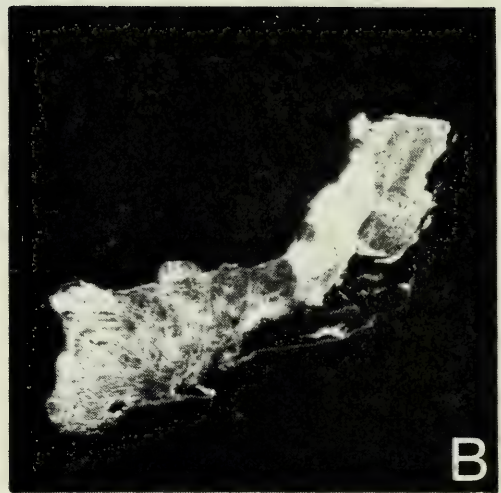
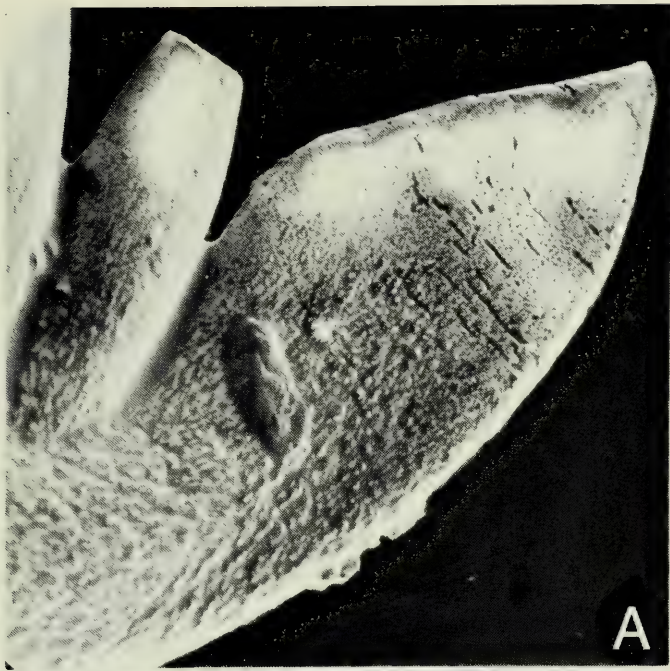
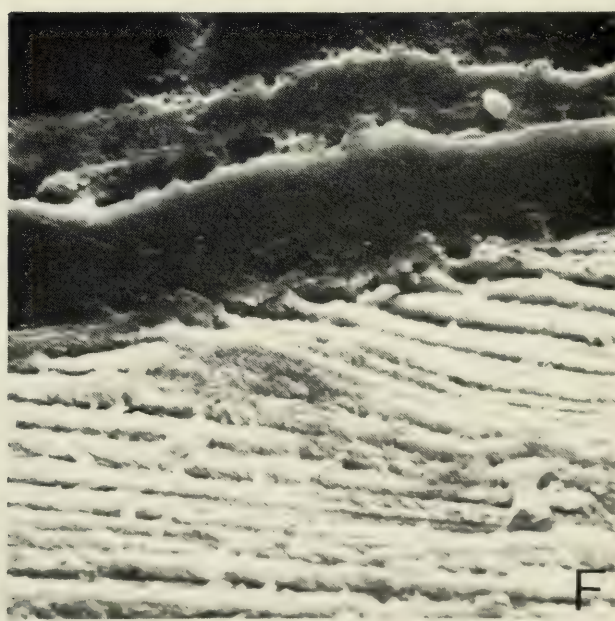
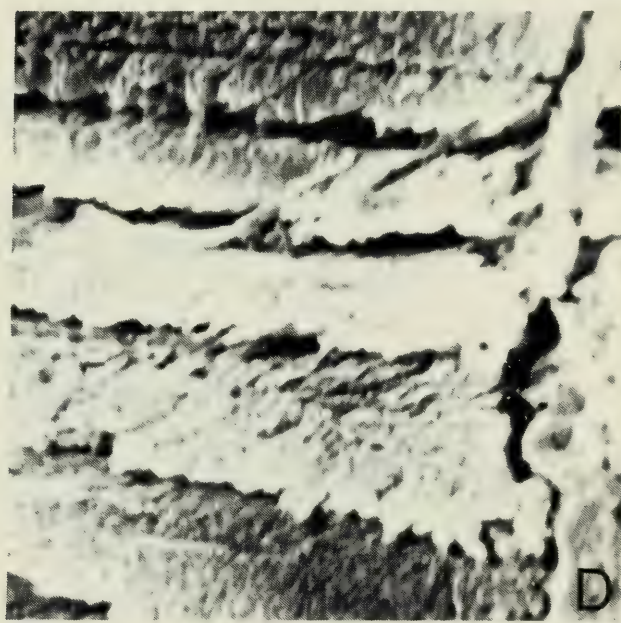
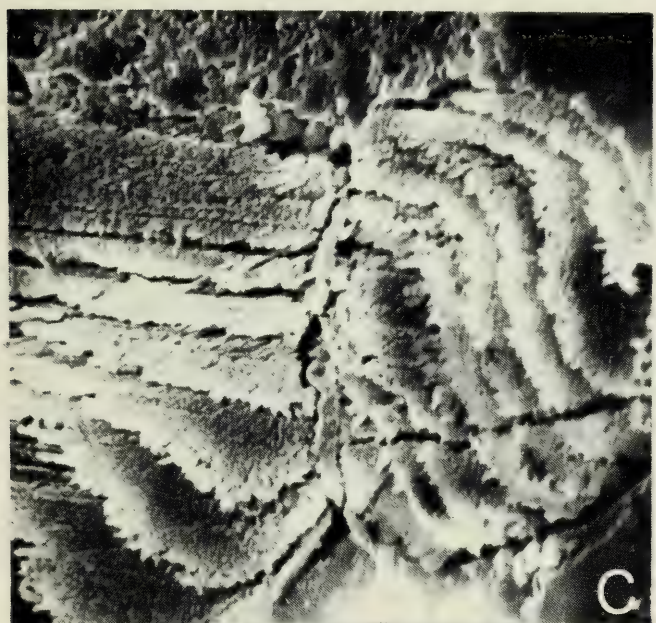
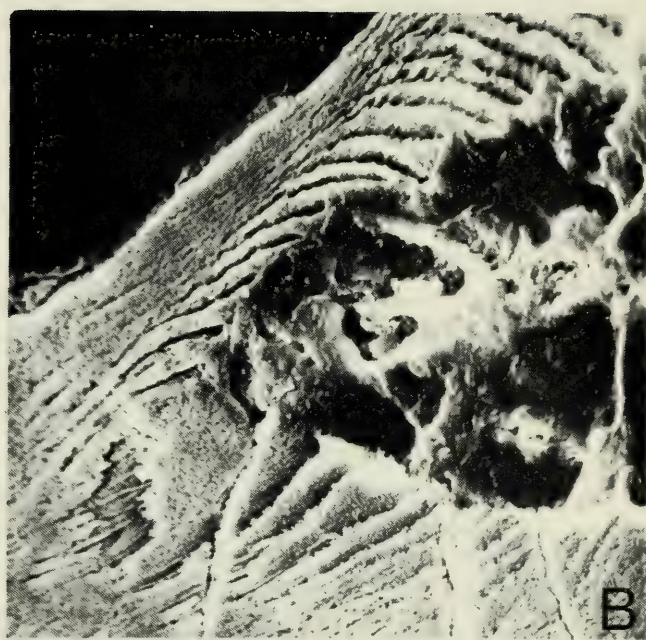
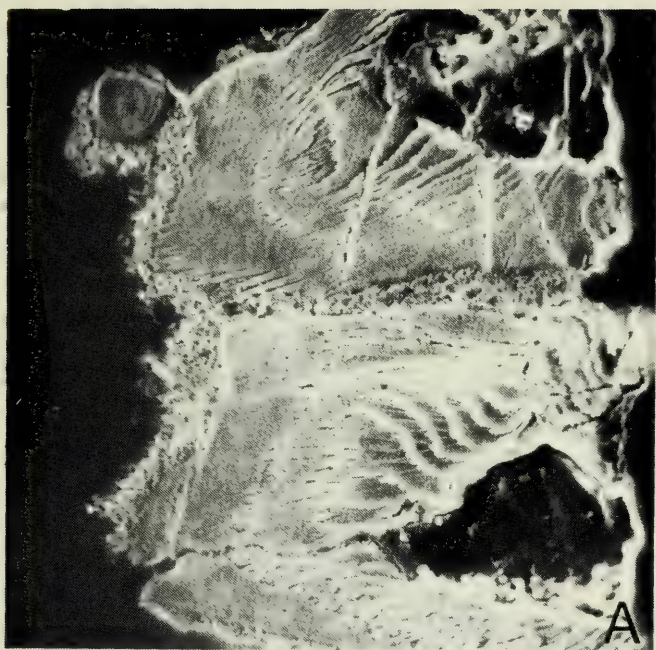


Fig. 11 A-D—Belodina sp. A. Farr Formation, Upper Ordovician, Lake Timiskaming outlier, Ontario. A) general view of longitudinal section revealing basal region with bifid cavity, heel region at top, anterior margin at bottom, lateral furrow passing horizontally in centre. Note interdigitating pattern on lamellar surfaces above tip of lower cavity; lamellae below lower cavity intersect anterior margin, $\times 325$. B) detail of upper cavity illustrated in Fig. 11A. Note how lamellae curve toward basal cavity, becoming several times thicker and developing wider interlamellar spaces, $\times 650$. C) detail of area above lower cavity shown in Fig. 11A. Note incurving of lamellae towards basal cavity; granular texture (crystallites?) of lamellae but with a diagonal (upper right to lower left) lamination in some at 30° to interlamellar spaces; interdigitating pattern seen at lower right, $\times 1,300$. D) details of centre of Fig. 11C to show granular texture of lamellae and apparent lamination, $\times 3,250$.

E-F—*Belodina*, sp. B. Farr Formation, Upper Ordovician, Lake Timiskaming, Ontario. E) general view. Longitudinal section, lamellar structure except in denticles; longitudinal furrow prominent, $\times 115$. F) detail of area shown in Fig. 11E at central lower edge of basal cavity. Lamellar structure; lamellae progressively overlap earlier deposited ones as basal cavity is enlarged; some lamellae varying in thickness; apparent inclined lamination of crystallites within lamellae as shown in Fig. 11C, $\times 1,125$.



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